ABUNDANCE OF SOUTHERN CALIFORNIA COASTAL BOTTLENOSE DOLPHINS ESTIMATED FROM TANDEM AERIAL SURVEYS

J. V. Carretta
K. A. Forney

Southwest Fisheries Science Center, NMFS,
P. O. Box 271, La Jolla, California 92038, U.S.A.
E-mail: jim.carretta@noaa.gov

J. L. Laake

National Marine Mammal Laboratory,
Alaska Fisheries Science Center, NMFS,
7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

Abstract

We describe a tandem aerial survey method for bottlenose dolphins (*Tursiops truncatus*) that uses two aircraft and independent observer teams to conduct consecutive surveys of the same coastal strip one hour apart. Alternatively, one aircraft with one observer team surveys the same coastal strip twice over several hours. Using mark-recapture analysis, we corrected survey counts for visibility bias resulting from missing dolphin groups at the surface and submerged groups. Dolphin groups were considered "recaptured" when we determined that both observer teams had detected the same group. This tandem method is highly useful for estimating abundance (and visibility bias) for species where population closure may be assumed between flights. We assumed population closure between flights and matched groups using geographic location, group size, and expected travel rates. We derive a new variance estimator of population size which incorporates group-size variability commonly encountered in cetacean surveys. From six tandem surveys conducted from 1991 to 1994, we estimated the abundance of southern California coastal bottlenose dolphins to be between 78 (95% CI 60–102) and 271 (240–306) animals, with an average of 140 (128–154). Variability in abundance estimates is likely due to seasonal and interannual movement of animals along the California and Baja California coast. Abundance estimates from tandem surveys averaged 53% higher than dolphin counts obtained from individual survey flights, demonstrating the importance of correcting for visibility bias.

Key words: coastal bottlenose dolphins, *Tursiops truncatus*, California, abundance, tandem aerial survey, double-count, mark-recapture, visibility bias.

Aerial surveys of dolphins will typically yield underestimates of abundance because observers fail to detect dolphin groups that are submerged or are

overlooked because of observer inexperience, fatigue, or adverse survey conditions such as sun glare or rough seas. Marsh and Sinclair (1989) coined the terms availability and perception bias, respectively, for these forms of visibility bias. Simultaneous double-count surveys can be used with mark-recapture models to correct for perception bias (Pollock and Kendall 1987, Estes and Jameson 1988, Graham and Bell 1989, Marsh and Sinclair 1989, Potvin *et al.* 1992, Buckland *et al.* 1993, Rivest *et al.* 1995, Manly *et al.* 1996). Surveys of this type generally rely on two independent observers or observer teams to conduct simultaneous counts from the same aircraft or sighting platform. Because the counts are simultaneous, diving animals and animals obscured by turbid water may be missed by both observer teams. Thus, correction factors for availability bias must be constructed from a model of the animal's diving behavior (Barlow *et al.* 1988, Marsh and Sinclair 1989). Alternatively, tandem surveys separated sufficiently in time provide double-counts that can be used to correct for availability and perception bias (Buckland and Turnock 1992; Cockcroft *et al.* 1992; Palka 1995; Laake *et al.* 1997; Hiby and Lovell, in press). The tandem survey we describe represents an extension of the experimental methods of Cockcroft *et al.* (1992) and the mathematical applications of Potvin *et al.* (1992) and Rivest *et al.* (1995).

From 1991 to 1994 we conducted six tandem aerial surveys to estimate the abundance of coastal bottlenose dolphins (*Tursiops truncatus*) in southern California. Coastal bottlenose dolphins are primarily found within 1 km of shore and, based on previously published morphological and behavioral data (Walker 1981, Hanson and Defran 1993), demonstrate little or no interchange with the offshore population of California bottlenose dolphins. The most recent estimates of abundance for the coastal population are over a decade old and are based on photographic mark-recapture data collected between 1981 and 1986 (Hansen 1990, Hansen and Defran 1990). We present more recent abundance estimates from six tandem aerial surveys using double-counts to correct for visibility bias. We also derive a new variance estimator for population size which incorporates the group size variability commonly encountered in cetacean surveys (Appendix). In addition, we summarize the results from 16 non-tandem and incomplete tandem surveys conducted from 1990 to 1994.

MATERIALS AND METHODS

Field Methods

Our main study area extended from the U.S./Mexico border (32°32'N) to Point Conception (34°27'N), along approximately 450 km of coastline (Fig. 1), hereafter referred to as the Southern California Coastline or SCC. One survey extended farther north to Monterey Bay (815 total km of coastline). The survey aircraft were twin-engine Partenavia P-68s, flown at an altitude of 213 m (700 ft) and an airspeed of 185 km h^{-1} (100 kn)[1]. Surveys were flown

---

[1] A NOAA DeHavilland Twin Otter aircraft with an equivalent viewing configuration was used for two surveys conducted in April 1991.
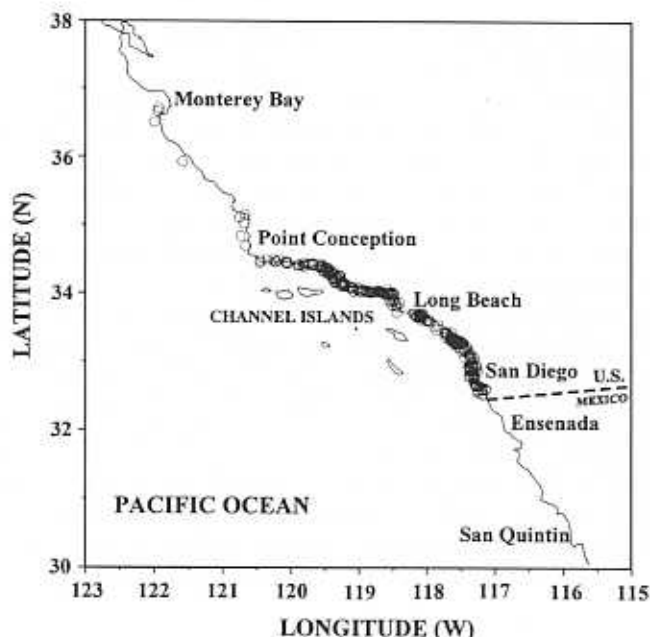
Figure 1. Map of study area, including location of all 277 sightings (○) of coastal bottlenose dolphins. Only one survey conducted between Point Conception and Monterey Bay.

at a distance of 300 m from the shore (calibrated using a clinometer), although occasionally, the distance increased to near 500 m when maneuvering around points, coves, and bays along the coast. We chose this distance to maximize the sighting efficiency of observers, based on independent observations that coastal bottlenose dolphins in southern California are found within 250 m of shore 90% of the time and within 500 m of shore 99% of the time (Hanson and Defran 1993). Surveys were conducted in Beaufort sea states 0–4 with clear or mostly clear skies (<50% cloud cover). In addition to the pilot, a team of three observers and one data recorder was present on all flights. Two observers, positioned on the inshore and offshore sides of the aircraft, respectively, searched beneath and to the sides of the aircraft through bubble windows. The inshore observer searched from the trackline (flight path) to the shore. Although the offshore observer's field of view extended well offshore, this observer concentrated searching effort within 300 m of the trackline to maximize sighting efficiency. A third observer searched through a window in the belly of the aircraft and searched from the trackline out to 150 m perpendicular distance. All three observers reported sighting and environmental data directly to the data recorder, who entered the information into a laptop computer linked to the aircraft's navigational system. When dolphins were detected, the observer(s) informed the data recorder and then the plane circled over the dolphin group, generally for 5–15 min. The aircraft made several passes over the group to allow the three observers and data recorder to count

the number of animals present. The highest actual count was reached by consensus and entered into the sighting record.

We conducted surveys on 22 dates between 1990 and 1994. Six complete tandem surveys were flown, whereas all others consisted of single-aircraft surveys or incomplete tandem surveys where only a portion of the total coastline was surveyed. Five of the complete tandem surveys used two aircraft and observer teams, which surveyed the same coastal strip approximately one hour or 185 km apart. This distance was chosen to maintain a safe distance between the two aircraft because of the need to circle over dolphin groups for up to 15 min and to prevent visual contact or cuing of the trailing team to groups detected by the leading team. A sixth complete tandem survey used one aircraft and observer team that surveyed north and southbound legs of the coastline several hours apart. Only the six complete tandem surveys were used in the mark-recapture analysis. For the five two-aircraft tandem surveys, the lead aircraft was identified as *flight 1* and the trailing aircraft as *flight 2*. The observer team on *flight 2* was not aware of the numbers or locations of dolphins seen during *flight 1*. For the sixth single-aircraft tandem survey, the northbound leg was designated *flight 1* and the southbound leg *flight 2*.

Analytical Methods

In the field we recorded aggregations of dolphins as "sightings." Sightings usually consisted of animals within several body lengths of each other. Frequently, several aggregations in apparent association (subgroups) were found within 0.5–2 km (less than a minute of flight time) of each other. Rarely, these subgroups were evenly spaced over a distance of up to 6–8 km (2–3 min flight time). At the analysis stage, these subgroups of "associated" animals were pooled and defined as one "group." We combined subgroups because our data suggested that splitting and merging of subgroups frequently occurred between flights, and we also observed such behavior while counting animals. Approximately one-third of our groups, as defined, are the result of subgroup pooling. All dolphin groups detected during *flight 1* (by observer team 1) were considered "marked." Groups were considered "recaptured" if we determined that the same group (or part thereof) was detected during *flight 2* (by observer team 2).

Our study did not rely on simultaneous counts, so we had to make assumptions about group travel speeds to determine which groups were recaptured. We considered groups detected during flights 1 and 2 to be unique (not recaptured) if the distance between them would have required the group to exceed an assumed *maximum group travel speed* between the time of the two encounters. We chose a maximum group travel speed of 9.3 km h^{-1} (5 kn), based on prior information about dolphin travel speeds and observations of relatively fast traveling groups detected during our study. Au and Perryman (1982) have shown that pelagic dolphins of the genus *Stenella* traveled from 9.4 to 16.3 km h^{-1} (5.1 to 8.8 kn) when actively avoiding research vessels. Most reports of bottlenose dolphin travel speeds are between 1 and 6 km h^{-1}

(0.6 to 3.2 kn) (Irvine *et al.* 1981, Cockcroft *et al.* 1992, Mate *et al.* 1995). Cockcroft *et al.* (1992) suggested an upper speed of 6 km h^{-1} (3.2 kn) for coastal bottlenose dolphins off South Africa, and these authors used an average group travel speed of 3.5 km h^{-1} (1.9 kn) as their "critical speed" in a similar mark-recapture analysis. Because the choice of a maximum group travel speed is somewhat arbitrary, we completed a sensitivity analysis, using four maximum group travel speeds of 3.7, 5.5, 7.4, and 9.3 km h^{-1} (2, 3, 4, and 5 kn) to test the effect of each speed on our abundance estimates. Reducing the assumed maximum group travel speed would result in fewer "recaptured" groups between flights, thus increasing the abundance estimates and *vice versa*. We emphasize group capture data for the maximum group travel speed of 9.3 km h^{-1}, because these data provide the most conservative estimates of abundance.

Observed group size was used as a second factor in the determination of group recaptures. Sightings detected on both flights in geographical proximity to one another were only considered recaptured if the smaller count was at least 50% of the larger one. An example from our data is a group of 32 animals detected during flight 1 that we considered a separate group from a sighting of one dolphin detected during flight 2 at nearly the same location 2.1 h later. Even if the single dolphin was previously observed as part of the group of 32, effectively a "group" of 31 animals was missed by observer team 2. Considering the two observations of 1 and 32 animals as a recapture would result in an overestimate of the detection probability. Although we cannot be 100% certain about all recaptures, we are confident that geographic position, expected maximum group travel speed, group size, and the tendency of groups to remain within the narrow coastal strip covered by our flights serve as four good criteria on which to base recaptures. We believe very few dolphins exited or entered the study area to and from offshore areas, and we have assumed population closure between the two flights. Confidence in our recaptures is bolstered by the fact that encounter rates of bottlenose dolphins along the coastline were quite low (2.25 sightings/100 km searched).

Small sections of our study area (<10% of the total), such as coastal airport traffic-control regions, were frequently inaccessible to one or both flights. Occasionally, one of the two flights was permitted access to a segment unavailable to the other flight. Dolphin groups seen in these situations were systematically omitted from our mark-recapture analysis, as were all groups seen during periods of non-trackline effort (*i.e.*, off-effort sightings).

Estimation of Detection Probability and Correction Factors

Dolphin groups were classified into two size strata denoted by the subscript h; small groups of 1–10 animals ($h = 1$) and large groups of 11 or more ($h = 2$). This stratification split our sample approximately in half and is identical to a group size stratification used to estimate the detection probability of dolphin groups on previous aerial surveys in California (Forney *et al.* 1995). When observer team counts of recaptured groups differed slightly (*e.g.*, 12

animals *vs.* 9), the higher count was used to determine the group size stratum (Potvin *et al.* 1992).

Let n_{hk} represent the number of groups of size stratum h, that were seen only by observer team 1 ($k = 1$), only by observer team 2 ($k = 2$), or by both observer teams ($k = 3$). The estimators for the probabilities (p_{hk}) of detecting a group in size stratum h by each observer team ($k = 1$ and $k = 2$, respectively) are:

$$\hat{p}_{h1} = \frac{n_{h3}}{n_{h2} + n_{h3}} \quad \text{and} \quad \hat{p}_{h2} = \frac{n_{h3}}{n_{h1} + n_{h3}} \tag{1}$$

These estimators assume the capture (detection) probabilities are different for the two flights. This is equivalent to the Lincoln-Petersen approach (Seber 1982) and to model M_t of Otis *et al.* (1978).

Within each stratum h, we estimated a visibility bias correction factor (c_h) for groups missed by both observer teams. The correction factor is defined as the inverse of the probability that a dolphin group in size stratum h is seen by at least one observer team. This correction factor is applied to the total count of unique groups seen ($n_h = n_{h1} + n_{h2} + n_{h3}$) to provide an estimate of the total number of groups in the study area. The estimator for the correction factor is (Rivest *et al.* 1995):

$$\hat{c}_h = \frac{1}{1 - [(1 - \hat{p}_{h1})(1 - \hat{p}_{h2})]} = 1 + \frac{n_{h1}n_{h2}}{n_h n_{h3}}. \tag{2}$$

We used the bias-corrected version (Rivest *et al.* 1995) which is equivalent to the bias-correction for the Lincoln-Petersen estimator derived by Chapman (1951):

$$\hat{c}_h = 1 + \frac{n_{h2}n_{h1}}{n_h(n_{h3} + 1)}. \tag{3}$$

The variance of $\hat{c}_h$ is (Rivest *et al.* 1995):

$$v(\hat{c}_h) = \frac{n_{h2}^2 n_{h1}^2}{n_h^2(n_{h3} + 1)^2} - \frac{n_{h2}(n_{h2} - 1)n_{h1}(n_{h1} - 1)}{n_h(n_h - 1)(n_{h3} + 1)(n_{h3} + 2)}. \tag{4}$$

We calculated the values of $\hat{p}$, $\hat{c}_h$, and $v(\hat{c}_h)$ by pooling the n_{hk} values from six tandem surveys. Such pooling was necessary due to the relatively small number of groups detected on each tandem survey, which, in some cases, would have resulted in zero recaptures. Rivest *et al.* (1995) recommend that small strata, with less than six groups seen by both observer teams, be avoided. When calculating the values of $\hat{p}$, $\hat{c}_h$, and $v(\hat{c}_h)$, it is important to note that dolphin *groups*, and not the number of individuals, are the analysis units (Rivest *et al.* 1995).

Estimation of dolphin abundance, $\hat{T}$

Let a_{hk} represent the number of animals in group size stratum h counted by observer team k. The double-count, or the total number of animals seen

during a tandem survey (a_h), is determined by adding the number of animals seen by both observer teams (a_{h3}) to those seen exclusively by observer teams 1 (a_{h1}) and 2 (a_{h2}). For a given survey, the estimator of total dolphin abundance $\hat{T}$ is (Rivest *et al.* 1995):

$$\hat{T} = \sum_{h=1}^{2} \frac{\hat{c}_h a_h}{f} = \sum_{h=1}^{2} \frac{\hat{c}_h n_h \bar{g}_h}{f} \tag{5}$$

where f is the fraction of the area sampled, and $\bar{g}_h = a_h/n_h$ is the mean group size in stratum h.

In their study of deer populations, Potvin *et al.* (1992) and Rivest *et al.* (1995) randomly selected survey parcels (i) and extrapolated observed deer densities to the total study area. For our surveys, we omit the parcel subscript i from our formulae because our sampling fraction, f, is treated as one, because virtually the entire study area was surveyed each time.

The variance of $\hat{T}$ derived by Rivest *et al.* (1995) did not account for group size variability within stratum h, because the number of deer in a group of size h was constant. In our study we do not have complete stratification of group sizes, because our small groups ($h = 1$) are defined as containing 1–10 animals and large groups ($h = 2$) contain 11 or more. Rivest *et al.* (1995) derived a variance formula that contains three terms: σ_r^2 (variance due to random selection of survey parcels), σ_p^2 (binomial variation in the number of animals seen), and σ_c^2 (variance in the population estimate due to the estimation of correction factors $\hat{c}_h$). A fourth term, σ_g^2, which incorporates the within-stratum variance in group size has been added for our study. Because we surveyed the entire area (*i.e.*, $f = 1$), the first term, σ_r^2, drops out of the variance calculation and $v(\hat{T})$ is reduced to:

$$v(\hat{T}) = \sigma_p^2 + \sigma_c^2 + \sigma_g^2 \tag{6}$$

The recommendation of Rivest *et al.* (1995) for incorporating group size into the variance is incorrect and could substantially underestimate σ_p^2. The correct formulation of the variance with all four components is derived in the Appendix.

RESULTS

Between 1991 and 1994 we surveyed a total of 11,940 km and recorded 277 bottlenose dolphin sightings (Fig. 1). Of these, 269 sightings were recorded while on survey effort, and the remaining eight sightings were made while off effort. Total dolphin counts by a single observer team for all completed surveys were highly variable, ranging from 38 to 215 animals (Table 1). Overall mean dolphin encounter rates were 2.25 sightings/100 km and 48.8 animals/100 km. Of 269 on-effort sightings, 234 (87%) were detected either inshore of, or on, the trackline, demonstrating the dolphins' strong association with surf zone habitat (Fig. 2).

During the six tandem surveys, 5,377 km were surveyed and 107 sightings of bottlenose dolphins were recorded. After pooling sightings of closely asso-

Table 1. Summary of aerial surveys conducted on 22 dates between 1990 and 1994. Information from six tandem surveys used in our mark-recapture analysis shown in bold.

Date	Maximum dolphin count	Survey type	Total km surveyed
23 May 1990	42	single-aircraft	429
3 April 1991	6	single-aircraft (incomplete)	236
5 April 1991	44	single-aircraft	432
12 June 1991	65	single-aircraft	415
29 August 1991	**60**	**tandem flight 1**	**251**
29 August 1991	**66**	**tandem flight 2**	**311**
25 October 1991	215	tandem flight 1	440
25 October 1991	118	tandem flight 2 (incomplete)	269
21 December 1991	147	single-aircraft	456
22 December 1991	147	single-aircraft	438
25 February 1992	181	single-aircraft	403
26 February 1992	157	single-aircraft	380
21 April 1992	195	single-aircraft	402
22 April 1992	117	single-aircraft	427
21 July 1992	**56**	**tandem flight 1**	**431**
21 July 1992	**64**	**tandem flight 2**	**417**
22 July 1992	38	single-aircraft	435
21 May 1993	30	single-aircraft (incomplete)	130
2 June 1993	**211**	**tandem flight 1**	**415**
2 June 1993	**108**	**tandem flight 2**	**425**
3 June 1993	118	single-aircraft	402
13 July 1993	**99**	**tandem flight 1**	**442**
13 July 1993	**120**	**tandem flight 2**	**440**
14 July 1993	**57**	**single-aircraft**	**431**
10 August 1993	**91**	**tandem flight 1**	**419**
10 August 1993	**97**	**tandem flight 2**	**429**
11 August 1993	57	single-aircraft	448
25 July 1994[a]	145	tandem flight 1	634
25 July 1994[a]	107	tandem flight 2	763

[a] Survey extended north to Monterey Bay.

ciated animals into *groups*, the 107 *sightings* were redefined as 61 dolphin *groups*, accounting for the splitting and coalescing of subgroups at the maximum group travel speed of 9.3 km h^{-1} (Table 2). Of the 61 groups, 28 (46%) were seen by both observer teams and 33 (54%) were not recaptured. Of the 33 groups not recaptured, 26 (79%) were small groups of 1–10 animals. Of the 28 recaptured groups, 17 (61%) were large groups of 11 or more animals. Differences between observer team counts for the 28 recaptured groups were small but increased with group size (Fig. 3). Observed group size was highly variable, ranging from 1 to 99 animals ($\bar{x} = 13.0$, SD $= 14.1$). The mean probability, $\hat{p}$, of detecting a group by one observer team was estimated as 0.47 for groups of 1–10 animals and 0.84 for groups of 11 or more (Table 2). The visibility bias correction factor was estimated as 1.36 (CV $= 0.12$) for
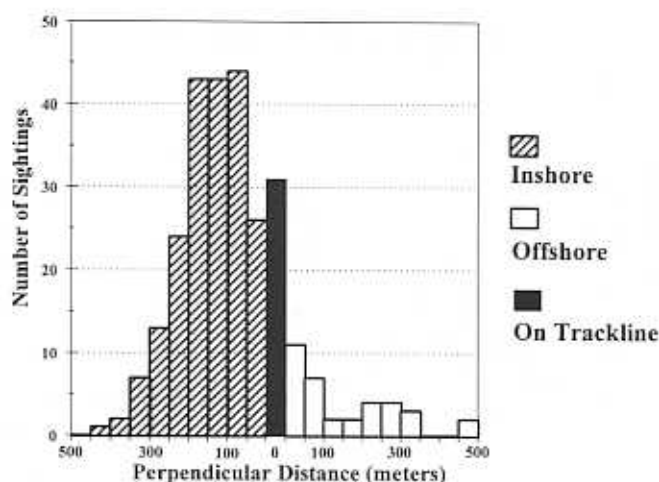
Figure 2. Perpendicular sighting distances for 269 on-effort dolphin groups.

small groups of 1-10 animals and 1.01 (CV = 0.013) for groups of 11 or more (Table 2).

Abundance estimates ($\hat{T}$), evaluated at a maximum group travel speed of 9.3 km h^{-1}, were highly variable and ranged from 78 (95% CI 60–102) to 271 (240–306) animals (Table 3). The mean number of dolphins utilizing the SCC over the six tandem surveys was 140 (95% CI 128–154). Double-counts (a_k) averaged 41% higher (range from six tandem surveys = 20%–62%) than mean counts obtained by a single observer team, where the mean count was calculated as $[(a_{b1} + a_{b3}) + (a_{b2} + a_{b3})]/2$. Abundance estimates averaged 53%

Table 2. Summary of dolphin groups detected on six tandem surveys by each observer team evaluated at four maximum group-travel speeds. Given are number of groups of size category b detected by observer team 1 only (n_{b1}), team 2 only (n_{b2}), by both teams (n_{b3}), and collectively (n_b). Also shown are sighting probabilities p, for each observer team, mean sighting probability $\bar{p}$, group correction factor ($\hat{c}_b$) calculated from Equation 3, and variance $v(\hat{c}_b)$ of correction factor calculated from Equation 4.

| Travel speed	n_{b1}	n_{b2}	n_{b3}	n_b	p_{b1}	p_{b2}	$\bar{p}_b$	$\hat{c}_b$	$v(\hat{c}_b)$
Small groups (1–10)									
9.3 km/h	10	16	11	37	0.41	0.52	0.47	1.36	2.6×10^{-2}
7.4 km/h	12	17	10	39	0.37	0.45	0.41	1.48	4.3×10^{-2}
5.5 km/h	13	17	10	40	0.37	0.44	0.40	1.50	4.6×10^{-2}
3.7 km/h	17	24	6	47	0.20	0.26	0.23	2.24	0.30
Large groups (>10)									
9.3 km/h	6	1	17	24	0.94	0.74	0.84	1.01	1.9×10^{-4}
7.4 km/h	6	2	16	24	0.89	0.73	0.81	1.03	5.1×10^{-4}
5.5 km/h	8	4	14	26	0.78	0.64	0.71	1.08	2.4×10^{-3}
3.7 km/h	11	8	10	29	0.56	0.48	0.52	1.28	1.9×10^{-2}

Recaptured Group Counts
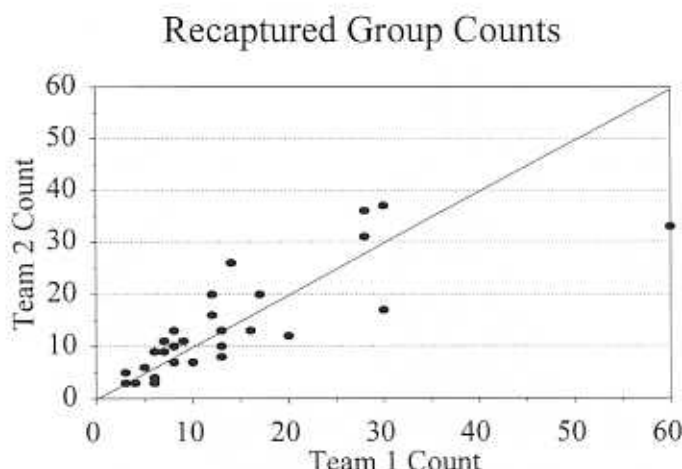
Figure 3. Comparison of 28 recaptured group counts by observer team. Solid line represents 1:1 count ratio.

higher (range = 39%–73%) than mean counts obtained by a single observer team and 9% higher (range = 5%–17%) than double-counts.

Abundance estimates increased when the assumed maximum group travel speed was decreased. This effect was purely analytical, as fewer groups were considered recaptured at lower speeds. The difference in estimates obtained over the maximum group-travel speed range of 5.5–9.3 km h^{-1} was negligible, but increased in most cases when the maximum group-travel speed was reduced to 3.7 km h^{-1} (Fig. 4a–f). Evaluated at a maximum group-travel speed of 3.7 km h^{-1}, abundance estimates for the six tandem surveys ranged from 115 (95% CI 65–202) to 369 (95% CI 235–580) dolphins, with an average of 227 (95% CI 173–298). We believe that estimates obtained at this maximum group travel speed are positively biased for reasons given in the Discussion section.

DISCUSSION

Geographic Range

California coastal bottlenose dolphins regularly occur within 1 km of shore from Ensenada, Mexico (31°52′N) to Monterey Bay, California (37°00′N), with groups occasionally seen as far north as the San Francisco Bay area (37°40′N) (Hansen 1990, Hansen and Defran 1990, Wells *et al.* 1990, Feinholz 1996). A stranding record of a coastal bottlenose dolphin 100 km north of Seattle, Washington represents the northernmost occurrence for this population (Ferrero and Tsunoda 1989). Animals photographed near San Diego have been resighted 670 km to the north in Monterey Bay (Wells *et al.* 1990) and movement of individuals between Orange County, California (33°40′N) and Ensenada, Mexico, has been documented (Defran *et al.* 1986). The region

between Ensenada and San Quintín, Mexico (30°30′N) has been tentatively proposed as the southern boundary of the population, based on the rarity of photographic recaptures between San Quintín and Ensenada (Caldwell 1992).

Because our surveys covered only a portion of the coastal bottlenose dolphin's north-to-south range, our abundance estimates should not be taken to represent the population total, but rather only those animals utilizing the SCC on a given survey date. The survey from which we obtained our highest estimate of abundance, 271 (95% CI 240–306), covered approximately half of the population's known range, and the number of animals outside the surveyed area is unknown.

Comparison with Previous Estimates

Based on photographic mark-recapture surveys conducted from 1981 to 1983, Hansen (1990) estimated 240 (95% CI 120–477) coastal bottlenose dolphins for San Diego County, from a total of 123 identified individuals. From 1984 to 1986, another photographic mark-recapture survey of the same area resulted in point estimates of 1,418 to 1,686 dolphins, from 215 identified individuals, but no level of statistical precision was given for these estimates (Hansen and Defran 1990). A comparison of the recapture data from each study revealed strong site fidelity of dolphins to San Diego county from 1981 to 1983 and minimal site fidelity from 1984 to 1986. Hansen and Defran (1990) proposed that the much higher 1984–1986 estimates resulted from a shift in the distribution or abundance of coastal bottlenose dolphins in southern California triggered by the 1982–1983 El Niño. This hypothesis is supported by the documented range expansion into central California following the 1982–1983 El Niño (Wells *et al.* 1990). Prior to this event the only records of bottlenose dolphins in central California consisted of cranial material dating to the 1800s collected in San Francisco Bay and Monterey Bay (Dall 1873, True 1889, Orr 1963). It is likely that the 1984–1986 estimates of 1,400–1,600 dolphins presented by Hansen and Defran (1990) were positively biased by low resighting rates associated with a decrease in site fidelity near San Diego precipitated by the El Niño. In fact, when photographs from the 1981–1983 and 1984–1986 surveys were pooled, only 264 animals with distinctive dorsal fins were found to have visited San Diego County between the years 1981 and 1986 (Defran *et al.* 1986).

A direct comparison of abundance estimates obtained with photographic mark-recapture surveys with those from our aerial surveys is complicated for a few reasons. First, there has been a well-documented range expansion of coastal bottlenose dolphins north into central California (Wells *et al.* 1990, Feinholz 1996). Secondly, over a decade has passed since the photographic surveys were conducted, during which time two El Niño events have occurred. Finally, our SCC survey area is much larger than the area for which photographic mark-recapture estimates were obtained. Despite these differences, the number of dolphins estimated by Hansen (1990) for the San Diego area (240, 95% CI 120–477) is similar to our highest estimate for the SCC (271, 95%

Table 3. Abundance estimates for southern California coast (SCC), evaluated at maximum group travel speed of 9.3 km h^{-1}. Shown are number of dolphins (*a*) detected in group size stratum *b* by observer team 1 only (a_{h1}), team 2 only (a_{h2}), mutually by both teams (a_{b3}), and total dolphins encountered ($a_{b.} = a_{h1} + a_{h2} + a_{b3}$) within stratum. Mean group size $\bar{g}$, abundance estimate $\hat{T}$, three variance terms, and log-normal 95% confidence intervals of $\hat{T}$ shown for each group size stratum.

Date and stratum	a_{h1}	a_{h2}	a_{b1}	$a_{b.}$	$\bar{g}$	$\hat{T}$	σ^2_p	σ^2_s	σ^2_g	L95%	U95%
29 August 1991											
h = 1	8	6	8	22	5.5	30	56.1	12.5	32.8	16	57
h = 2	32	4	12	48	24.0	48	11.4	0.4	0.5	42	55
All strata	40	10	20	70	11.7	78	67.5	12.9	33.3	60	102
21 July 1992											
h = 1	18	7	0	25	6.3	34	72.4	16.2	21.5	19	61
h = 2	0	24	33	57	19.0	58	10.8	0.6	1.7	51	66
All strata	18	31	33	82	11.7	92	83.2	16.8	23.2	73	116
2 June 1993											
h = 1	9	11	11	31	4.4	42	63.6	24.9	20.4	26	68
h = 2	139	71	17	227	56.8	229	127.7	9.8	37.8	205	256
All strata	148	82	28	258	23.5	271	191.3	34.7	58.2	240	306
15 July 1993											
h = 1	0	17	8	25	4.2	34	48.3	16.1	6.0	21	55
h = 2	26	16	65	107	21.4	108	22.7	2.2	3.7	98	119
All strata	26	33	73	132	12.0	142	71	18.3	9.7	123	163
10 August 1993											
h = 1	13	13	23	49	8.2	67	185.5	39.4	6.0	43	104
h = 2	3	9	52	64	21.3	65	13.5	0.8	5.7	57	74
All strata	16	22	75	113	12.6	132	199	40.2	11.7	104	167

Table 3. Continued.

Date and stratum	a_{b1}	a_{b2}	a_{b3}	a_b	$\bar{g}$	$\hat{T}$	σ^2_p	σ^2_z	σ^2_g	L95%	U95%
25 July 1994[a]											
h = 1	12	5	3	20	4.0	27	37.1	10.4	11.6	16	47
h = 2	37	3	59	99	16.5	100	16.2	1.9	3.0	91	109
All strata	49	8	62	119	10.8	127	53.3	12.3	14.6	110	146
6 surveys pooled[b]											
h = 1	60	59	53	172	5.4	234	428.6	769.2	115.6	173	316
h = 2	237	127	238	602	26.2	608	156.1	69.9	90.0	574	644
All strata	297	186	291	774	14.1	842	584.7	839.1	205.6	767	925

[a] Values for southern California coast (SCC) only. Including north to Monterey Bay, $\hat{T}$ = 171 (95% CI 147–197).
[b] Average number of dolphins along SCC = 842 dolphins/6 surveys = 140 (95% CI 128–154).
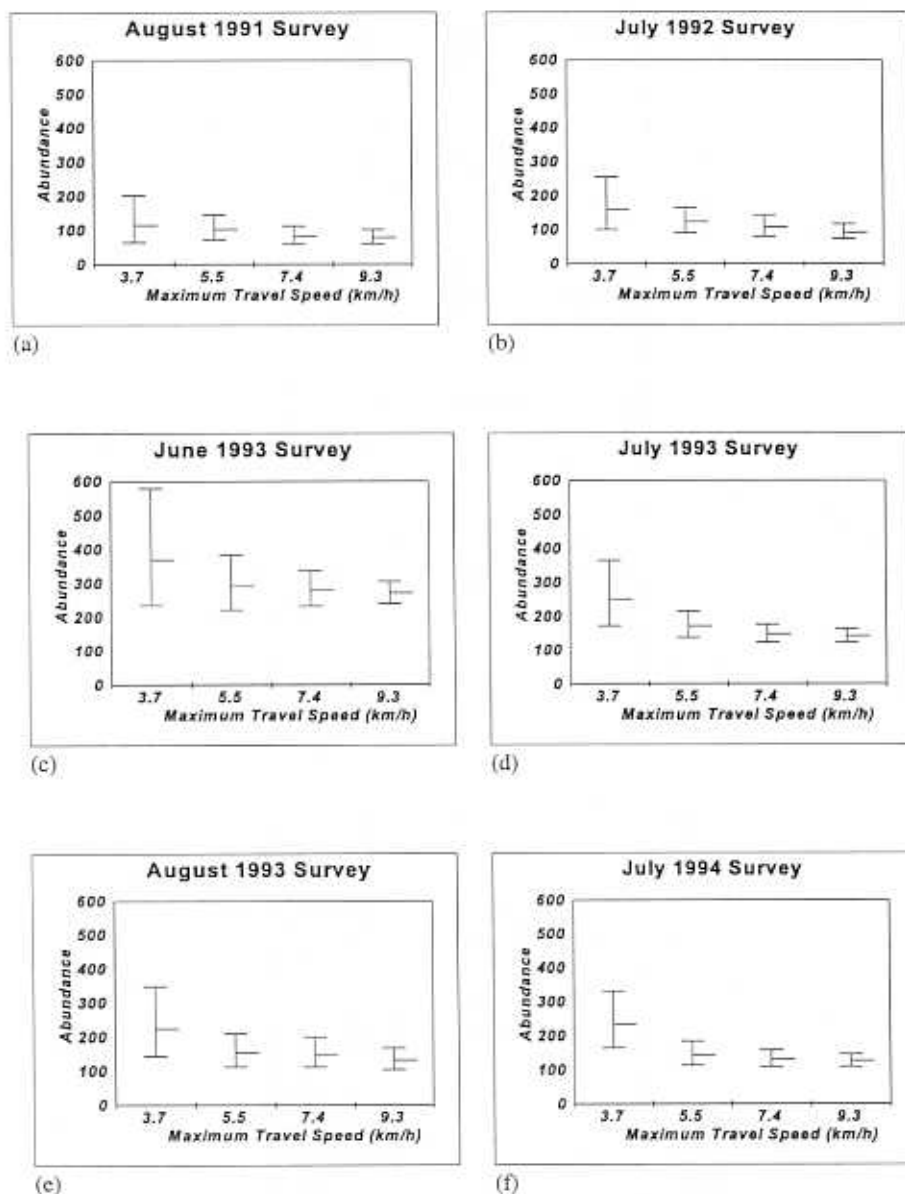
Figure 4(a–f). Estimates of abundance $\hat{T}$ and log-normal 95% confidence intervals for each of six tandem surveys evaluated at four maximum group-travel speeds. Estimates for the southern California coastline (SCC) only.

CI 240–306). Similarly, only 264 dolphins were photographically identified from the San Diego study area between the years 1981 and 1986, including animals that ranged south to Ensenada and north to Monterey Bay (Defran *et al.* 1986, Wells *et al.* 1990, Feinholz 1996). Taken together, these values

might suggest that the number of dolphins using the SCC has remained relatively stable over the last decade. This is plausible, given that many dolphins photographed near San Diego ranged throughout southern and central California, as well as south to Ensenada (Defran *et al*. 1986, Wells *et al*. 1990). However, such conclusions are confounded by the high variability in dolphin counts from our surveys, oceanographic changes associated with El Niño, and a relative lack of systematic survey coverage in central California and northern Baja California, Mexico. It should be noted that the only survey for which our survey effort extended north to central California yielded an estimate of 171 (95% CI 147–197) dolphins (Table 3), which is still less than our highest estimate obtained from the SCC; 271 (95% CI 240–306). A comparison of these two estimates makes it tempting to speculate about the size of the California-wide population, but any conclusions would be capricious, considering the high intersurvey variability of our estimates.

Survey Design and Analysis Considerations

Our analysis was based on the following assumptions: (1) the population was closed between the first and second flights, (2) detection probabilities were independent for each flight, and (3) recaptured groups were correctly matched. Population closure between flights was a reasonable assumption because bottlenose dolphins occupy a very narrow coastal strip and we surveyed a very long section of coast with only one hour (in one case several hours) between flights. However, the remaining two assumptions may not have been satisfied fully. The second assumption implies that detection probability is independent of observers, weather, the group's distance from the trackline, *etc*. We expect that perpendicular distance to the dolphin group will affect detection probability, but we assume that the perpendicular sighting distances (and detection probabilities) of groups seen between flights separated by an hour or more are independent, given that dolphin groups are likely to move within the survey strip between flights.

Accuracy in matching recaptured groups largely depends on our assumption about travel speed. Differences between abundance estimates obtained over the range of four maximum group travel speeds of 3.7 to 9.3 km h^{-1} were relatively small (Fig. 4a–f). The highest abundance estimate obtained at a maximum group travel speed of 3.7 km h^{-1} was 369 (95% CI 235–580), for a tandem survey conducted in June 1993. The corresponding estimate, assuming a maximum group travel speed of 9.3 km h^{-1}, was 271 (95% CI 240–306) dolphins. Despite differences between the two estimates, the smaller point estimate of 271 still falls within the 95% confidence interval (235–580) of the larger estimate. We believe that estimates obtained when assuming a maximum group travel speed of 3.7 km h^{-1} are positively biased, because bottlenose dolphins are capable of faster travel (Irvine *et al*. 1981, Cockcroft *et al*. 1992, Mate *et al*. 1995) and our recapture data indicates that many groups exceeded this rate over a period of an hour or more. When we limit the maximum group travel speed to 3.7 km h^{-1}, groups that travel faster than

this between the time of each flight will be analytically treated as not recaptured, when in fact they are recaptured. The advantage of assuming a maximum group travel speed of 9.3 km h^{-1} is that groups moving between 3.7 and 9.3 km h^{-1} can be correctly assigned as recaptured, while analytically having no effect on extremely slow-moving or stationary groups, which would already be considered recaptured at 3.7 km h^{-1}.

The tandem survey design we have presented is well suited to the population of California coastal bottlenose dolphins, but there are caveats to consider when designing such surveys for other species or geographical areas. Because California coastal bottlenose dolphins remain so close to the coast, our surveys essentially covered the entire habitat occupied by the animals. Therefore, it was unnecessary to estimate detection probabilities as a function of perpendicular distance or extrapolate animal densities to a larger area. This is clearly a unique situation and demonstrates the need to carefully examine assumptions when utilizing similar double-count methods for other species or geographic areas. In most aerial line-transect surveys only a proportion of a species' habitat will be surveyed, and effective strip width and animal densities may have to be estimated. However, mark-recapture methods can still be used to estimate visibility bias in conjunction with standard aerial line-transect surveys. For an illustration of such a combined line-transect and mark-recapture type experiment, we refer the reader to the work of Alpízar-Jara and Pollock (1996).

One should also consider the behavior and distribution patterns of the target species when deciding if double-counts should be simultaneous. In our study we were able to separate the two flights by 185 km or more because California coastal bottlenose dolphins inhabit such a narrow coastal strip, thus allowing us to assume population closure between flights. In addition, animal densities were quite low, which allowed us to confidently match groups seen an hour or more apart. In contrast, a double-count survey for a species such as the harbor porpoise (*Phocoena phocoena*), would require a simultaneous (or nearly so) double-count because harbor porpoise often occur at high densities, which would make matching of groups seen more than a few minutes apart tenuous. Also, the assumption of population closure (within a survey strip) between flights would likely be invalid for harbor porpoise, as their habitat is not as geographically restricted as that of California coastal bottlenose dolphins. For harbor porpoise a two-aircraft design would not suffice unless the aircraft were in close proximity (Hiby and Lovell, in press).

We estimated detection probabilities and visibility bias correction factors by pooling the results of six tandem surveys. When practical, survey-specific detection probabilities and correction factors should be estimated, because variables such as observer experience, animal densities, weather, tidal phase, and water turbidity may differ for each date (Marsh and Sinclair 1989). Pooling was necessary because the number of groups encountered on each survey was insufficient to avoid cases of zero recaptures or cases where a small number of recaptures (<6) would have severely biased the estimation of correction factors (Seber 1982, Rivest *et al.* 1995). In the future, tandem surveys will be ex-

tended north to central California, which may provide us with a sufficient number of recaptures to estimate survey-specific detection probabilities and correction factors. Failing this, we will continue to pool data from tandem surveys to estimate average probabilities and correction factors. We will likely base future abundance estimates on the average of a series of several tandem surveys, given that we have found dolphin counts to be highly variable between individual tandem surveys. This variability in dolphin numbers is likely due in part to variation in detection probabilities for each survey, as well as the movement of animals to and from Mexican waters.

The ability of tandem aerial surveys to provide corrected counts of coastal bottlenose dolphins over a large study area in a matter of several hours is encouraging. While photographic mark-recapture studies provide valuable information on the movements and life history of individuals, they often require years to collect sufficient data to estimate population size. We recommend that tandem aerial surveys continue to be used on a periodic basis to monitor the population of coastal bottlenose dolphins in California. Future surveys should be conducted throughout the year to determine if there are seasonal trends in abundance and distribution. Future surveys should be extended north to central California, and concurrent joint surveys with Mexico should be initiated to provide an abundance estimate for the entire population.

LITERATURE CITED

ALPÍZAR-JARA, R., AND K. H. POLLOCK. 1996. A combination line transect and capture-recapture sampling model for multiple observers in aerial surveys. Environmental and Ecological Statistics 3:311–327.

AU, D., AND W. L. PERRYMAN. 1982. Movement and speed of dolphin schools responding to an approaching ship. Fishery Bulletin, U.S. 80:371–379.

BARLOW, J., C. W. OLIVER, T. D. JACKSON AND B. L. TAYLOR. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: Aerial surveys. Fishery Bulletin, U.S. 86:433– 444.

BUCKLAND, S. T., AND B. J. TURNOCK. 1992. A robust line transect method. Biometrics 48:901–909.

BUCKLAND, S. T., J. M. BREIWICK, K. L. CATTANACH AND J. L. LAAKE. 1993. Estimated population size of the California gray whale. Marine Mammal Science 9:235–249.

CALDWELL, M. J. 1992. A comparison of bottlenose dolphins identified in San Quintín and the Southern California Bight. M.S. thesis, San Diego State University, San Diego, CA. 58 pp.

CHAPMAN, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1:131–160.

COCKCROFT, V. G., G. J. B. ROSS, V. M. PEDDEMORS AND D. L. BORCHERS. 1992. Estimates of abundance and undercounting of bottlenose dolphins off northern Natal, South Africa. South African Journal of Wildlife Research 22:102–109.

DALL, W. H. 1873. Descriptions of three new species of Cetacea from the coast of California. Proceedings of the California Academy of Sciences 5:12–14.

DEFRAN, R. H., D. L. KELLY, G. M. SHULTZ, A.C. WEAVER AND M. A. ESPINOZA. 1986. The occurrence and movements of the bottlenose dolphin in the Southern California Bight. Southwest Fisheries Center Administrative Report LJ-86-06C (unpublished). 26 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038.

ESTES, J. A., AND R. J. JAMESON. 1988. A double-survey estimate for sighting probability of sea otters in California. Journal of Wildlife Management 52:70–76.

FEINHOLZ, D. 1996. Pacific coast bottlenose dolphins (Tursiops truncatus gilli) in Monterey Bay, California. M.S. thesis, San Jose State University, Moss Landing Marine Laboratories, P. O. Box 450, Moss Landing, CA. 78 pp.

FERRERO, R. C., AND L. M. TSUNODA. 1989. First record of a bottlenose dolphin (Tursiops truncatus) in Washington State. Marine Mammal Science 5:302–305.

FORNEY, K. A., J. BARLOW AND J. V. CARRETTA. 1995. The abundance of cetaceans in California waters. Part II: Aerial surveys in winter and spring of 1991 and 1992. Fishery Bulletin, U.S. 93:15–26.

GRAHAM, A., AND R. BELL. 1989. Investigating observer bias in aerial survey by simultaneous double-counts. Journal of Wildlife Management 53:1009–1016.

HANSEN, L. J. 1990. California coastal bottlenose dolphins. Pages 403–420 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin, Academic Press, Inc., San Diego, CA.

HANSEN, L. J., AND R. H. DEFRAN. 1990. A comparison of photo-identification studies of California coastal bottlenose dolphins. Report of the International Whaling Commission (Special Issue 12):101–104.

HANSON, M. T., AND R. H. DEFRAN. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, Tursiops truncatus. Aquatic Mammals 19:127–142.

HIBY, L., AND P. LOVELL. In press. Using aircraft in tandem formation to estimate abundance of harbour porpoise. Biometrics.

IRVINE, A. B., M. D. SCOTT, R. S. WELLS AND J. H. KAUFMANN. 1981. Movements and activities of the Atlantic bottlenose dolphin, Tursiops truncatus, near Sarasota, Florida. Fishery Bulletin, U.S. 79:671–687.

LAAKE, J. L., J. CALAMBOKIDIS, S. D. OSMEK AND D. J. RUGH. 1997. Probability of detecting harbor porpoise from aerial surveys: Estimating g(0). Journal of Wildlife Management 61:63–75.

MANLY, B. F. J., L. L. MCDONALD AND G. W. GARNER. 1996. Maximum likelihood estimation for the double-count method with independent observers. Journal of Agricultural, Biological and Environmental Statistics 1:170–189.

MARSH, H., AND D. F. SINCLAIR. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

MATE, B. R., K. A. ROSSBACH, S. L. NIEUKIRK, R. S. WELLS, A. B. IRVINE, M. D. SCOTT AND A. J. READ. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphin (Tursiops truncatus) in Tampa Bay, Florida. Marine Mammal Science 11:452–463.

ORR, R. T. 1963. A northern record for the Pacific bottlenose dolphin. Journal of Mammalogy 44:424.

OTIS, D. L., K. P. BURNHAM, G. C. WHITE AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed populations. Wildlife Monographs No. 62. 135 pp.

PALKA, D. 1995. Abundance estimate of the Gulf of Maine harbor porpoise. Report of the International Whaling Commission (Special Issue 16):27–50.

POLLOCK, K. H., AND W. L. KENDALL. 1987. Visibility bias in aerial surveys: a review of estimation procedures. Journal of Wildlife Management 51:502–510.

POTVIN, F., L. BRETON, L.-P. RIVEST AND A. GINGRAS. 1992. Application of a double-count aerial survey technique for white-tailed deer, *Odocoileus virginianus*, on Anticosti Island, Québec. Canadian Field- Naturalist 106:435–442.

RIVEST, L.-P., F. POTVIN, H. CRÉPEAU AND G. DAIGLE. 1995. Statistical methods for aerial surveys using the double-count technique to correct visibility bias. Biometrics 51:461-470.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd. Ed. Macmillan Publishing, New York, NY.

TRUE, F. W. 1889. A review of the family Delphinidae. U.S. National Museum Bulletin 36:1–191.

WALKER, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Southwest Fisheries Center Administrative Report LJ-81-03C (unpublished). 52 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038.

WELLS, R. S., L. J. HANSEN, A. BALDRIDGE, T. P. DOHL, D. L. KELLY AND R. H. DEFRAN. 1990. Northward extension of the range of bottlenose dolphins along the California coast. Pages 421–432 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin, Academic Press, Inc., San Diego, CA.

APPENDIX

Rivest *et al.* (1995) provide a stratification scheme for reducing heterogeneity in the sighting probability of independent observers to estimate correction factors for visibility bias. For animals that aggregate into groups, Rivest *et al.* (1995) correctly state that "the group, not the animal, is the unit for estimating the correction factors." However, they incorrectly state that in the variance estimator group counts $n_{h\cdot}$ can be replaced with animal counts $n_{h\cdot}g_h$, where g_h is the group size. The substitution works for σ_r^2 and σ_e^2 but not for σ_p^2, which should be:

$$\frac{1}{f^2} \sum_{h=1}^{H} g_h^2 n_{\cdot h} \hat{c}_h(\hat{c}_h - 1).$$

Potvin *et al.* (1992) recognized that using animal frequencies in the variance estimator would underestimate the true variance, but their group sizes were small and the variance associated with sampling parcels (σ_r^2) was dominant. If group size is large, σ_p^2 would be severely underestimated by replacing group counts with animal counts. However, σ_p^2 will only become important if f is close to 1, which is obvious if we rewrite the variance given in eq 3.4 of Rivest *et al.* (1995) for $H = 1$ in terms of animal counts ($a_{\cdot\cdot} = n_{\cdot\cdot}g$) as:

$$v(\hat{T}) = \hat{T}^2\left(cv^2(\bar{n})[1 - cv^2(\hat{c})] + cv^2(\hat{c}) + f\left[cv^2(n_{\cdot\cdot}) - \frac{cv^2(\hat{c})}{n_{\cdot\cdot}}\right]\right), \qquad (A1)$$

where m parcels are sampled from a total of parcels $(f = m/M)$, $\bar{n} = n_{..}/m$, $\bar{a} = \bar{n} g$, and

$$\hat{T} = \frac{n_{..}\hat{c}g}{f} = M\bar{n}\hat{c}g = M\bar{a}\hat{c}$$

$$cv^2(\bar{n}) = (1 - f)\frac{\sum_{i=1}^{M} (n_{i.} - \bar{n})^2}{m(m - 1)\bar{n}^2}$$

$$cv^2(n_{..}) = \frac{\hat{c} - 1}{\hat{c}n_{..}}$$

$$cv^2(\hat{c}) = \frac{v(\hat{c})}{\hat{c}^2}.$$

The final term in (A1) represents the contribution from σ_p^2. The dominant terms will be $cv^2(\bar{n})$ and $cv^2(\hat{c})$ until a substantial portion of the area is surveyed (i.e., f approaches 1).

In addition, Rivest et al. (1995) did not address incomplete stratification of group size in which a single stratum contains groups of different sizes. They completely stratified by group size in their example, with each group being either a single or pair of deer. However, Potvin et al. (1992) applied the technique to a deer population and stratified by singles, pairs, and groups of three or more. In the latter stratum the average group size is a random variable and an additional component of variance is needed. For incomplete stratification of group size, the estimator for abundance is:

$$\hat{T} = \frac{M}{m} \sum_{h=1}^{H} n_{.h}\bar{g}_h\hat{c}_h = \frac{1}{f} \sum_{i=1}^{m} \hat{c}'a_{i.} = \frac{\hat{c}'a_{..}}{f},$$

where $\hat{c}'$ is the vector of correction factors for each stratum and $a_{.}$ is a vector of the total number of animals observed in each stratum. The variance estimator is the sum of the elements in Table A1 which replaces Table 1 in Rivest et al. (1995).

Table A1. Estimators of the variance compnents of double-count estimator with incomplete group size stratification.

Variance components	Estimator
σ_r^2	$\frac{(1 - f)M^2}{m(m - 1)}\left(\left[\sum_{i=1}^{m} (\hat{c}'a_{i.})^2 - a_{i.}'v(\hat{c})a_{i.}\right] - \frac{(a_{..}'\hat{c})^2 - a_{..}'v(\hat{c})a_{..}}{m}\right) - (1 - f)(\hat{\sigma}_p^2 + \hat{\sigma}_z^2)$
σ_p^2	$\frac{1}{f^2} \sum_{h=1}^{H} \bar{g}_h^2 n_{.h} (\hat{c}_h^2 - v(\hat{c}_h) - \hat{c}_h)$
σ_z^2	$\frac{a_{..}'v(\hat{c})a_{..}}{f^2}$
σ_k^2	$\frac{1}{f^2} \sum_{h=1}^{H} v(\bar{g}_h)n_{.h}^2 (\hat{c}_h^2 - v(\hat{c}_h) - \hat{c}_h)$

For complete stratification based on group size, $v(\bar{g}_h) = 0$ for each stratum and the additional term drops out. For a single correction factor (i.e., $H = 1$), (A1) becomes:

$$v(T) = \hat{T}^2 \left(cv^2(\bar{a})[1 - cv^2(\hat{c})] + cv^2(\hat{c}) + f\left[cv^2(n..) - \frac{cv^2(\hat{c})}{n..} \right] \right.$$
$$\left. + fcv^2(\bar{g})\left[\frac{c-1}{c} - cv^2(\hat{c}) \right] \right) \tag{A2}$$

where

$$cv^2(\bar{a}) = (1 - f) \frac{\sum\limits_{i=1}^{M} (a_{i.} - \bar{a})^2}{m(m-1)\bar{a}^2},$$

and

$$cv^2(\bar{g}) = \frac{\sum\limits_{i=1}^{n..} (g_i - \bar{g})^2}{n..(n.. - 1)\bar{g}^2}.$$

The final term in (A2) represents the contribution from σ_g^2, which also only becomes important as f approaches 1.